

Earthworms and Their Influence on Soil Structure and Infiltration

A.D. Tomlin, M.J. Shipitalo, W.M. Edwards, and R. Protz

I. Introduction	159
II. Earthworm Influences On Soil Structure	161
A. Effects on Porosity	161
B. Earthworm Burrows and Infiltration	162
C. Chemical Movement in Earthworm Burrows	162
D. Other Effects of Earthworms on Soil Structure	163
E. Ingestion and Casting Activity	165
III. Research Issues on Stability of Earthworm Casts	167
A. Methodological Issues Related to Measuring Stability	167
B. Concepts and Theories for Modeling Earthworm Cast Stability	171
C. Earthworm Casts and Soil Structure	172
IV. Research Imperatives	174
A. Solute Transport	174
B. Properties of Burrow Linings	175
C. Soil Processing and Soil Structure	175
D. Aggregate Stabilization	176
E. Field and Laboratory Studies	177
F. Organomineral Interactions and Soil Rehabilitation	177
References	177

I. Introduction

Edwards (1980) wrote that the consensus of evidence was that earthworms improve soil structure, fertility, organic matter decomposition, aeration and drainage. The processes by which these improvements occur are still open questions, especially their contribution to formation and maintenance of soil structure. The questions for soil scientists include: (1) What are the direct and indirect effects on soil structure at the microfabric scale? (2) What changes occur to water and air infiltration in soil? (3) What is the rate of turnover of organic and mineral matter? and (4) What is the contribution to soil aggregate stability? Additionally, questions arise with regard to the methods required for

characterizing biogenic soil structure, procedures for managing earthworm populations to increase their beneficial effects, and identifying the critical experiments needed to answer these questions.

Darwin's monograph (1881) was the first systematically documented attempt to relate earthworm activity with their effects on soil processes. He clearly understood that earthworms could, with time, bury large surface stones and features, and transport surface litter into soil via their casting activity. Darwin's descriptions were remarkably detailed at the scale of what today we would refer to as peds and landscapes. He realized that what is now called soil structure (in 1881, there was no formal notion of soil structure) is affected by the action of earthworms, for he says of them "...their chief work is to sift the finer from the coarser particles, to mingle the whole with vegetable debris, and to saturate it with their intestinal secretions" (Darwin 1881, pp. 174-175). This description is close to that of Lee (1985) who described the earthworm burrow lining as composed of illuviated material, dissolved materials, and earthworm secretions and excretions.

Bal (1974, 1982) demonstrated the contribution of faunal activity and soil structure by using micromorphological techniques to identify the characteristic features of fecal material from earthworms and other soil fauna. Altemuller and co-workers (Altemuller 1974, Altemuller and van Vliet-Lanoe 1990, Altemuller and Joschko 1992) used fluorescent staining techniques in combination with micromorphological methods to illustrate the spatial distribution of soil biota in the soil.

Different species of earthworms have different ecological strategies and behaviors (Bouché 1977) that take them to different compartments of the soil ecosystem. Anecic earthworms such as *Lumbricus terrestris* L. feed at the surface and transport surface litter vertically into the soil profile. Endogeic species such as *Aporrectodea turgida* Savigny are geophagous, obtaining their food by filtering it from the large amounts of soil that they pass as they burrow horizontally through surficial soil layers. Different earthworm behavior patterns and preferences for organic matter sources as food (Hendrikson 1990) have significant consequences for soil structure at the microfabric scale.

The production of earthworm channels by their burrowing habit has attracted attention of soil physicists because of the probability that this activity would strongly affect air and water infiltration into the soil (Ehlers 1975). An associated concern is changes in agrochemical leaching rates due to earthworm burrowing (Baker 1987, Shipitalo et al. 1990, Stehouwer et al. 1993). In some instances continuous no-tillage (NT) sites exhibit decreased surface run-off and increased infiltration and leaching relative to conventionally tilled (CT) sites (Edwards et al. 1988b). The issue is further complicated by earthworm burrow lining material which differs chemically (Tomlin et al. 1993) from surrounding matrix soil, and may influence solute transport through the burrows. Stehouwer et al. (1993) demonstrated that atrazine sorption and retention was up to three times greater on *L. terrestris* burrow walls than in an unlined void, and that

most of the difference in sorptive capacity was explained by organic carbon in the burrow linings.

This review covers three major topics, (1) earthworm influences on soil structure and infiltration, (2) mechanisms for aggregate (cast) stabilization, and (3) new approaches for characterizing earthworm cast stability.

II. Earthworm Influences On Soil Structure

A. Effects on Porosity

The readily measurable effects that earthworms have on porosity in soils are created by burrowing or surface and subsurface casting (Satchell 1967, Edwards and Loft 1977). In tilled soils, human activity may create changes that temporarily mask the effects of earthworms on porosity. However, in forests and grasslands, earthworm numbers have sometimes been correlated with higher porosity (Hoeksema and Jongerius 1959, Satchell 1967). Several authors report that introduction of earthworms to areas with no resident populations resulted in small increases in total porosity (Edwards and Loft 1977, Springett et al. 1992). Knight et al. (1992), however, reported that burrowing activity by introduced earthworms increased macroporosity in pastures.

No-tillage, unlike conventional practices, has been positively correlated with higher earthworm densities (Edwards and Loft 1982, Mackay and Klavivko 1985) and higher burrow density (Lal 1974, Ehlers 1975, Edwards and Loft 1982). In the early 1970's, several scientists counted earthworm burrow densities in the field (Lee 1985), and related number and size of burrows to air and water movement. Kretzschmar (1987) found as many as 10,000 *Allolobophora* spp. burrows per square meter, and Edwards et al. (1988a) reported 1.6 million *L. terrestris* burrows (≥ 5 mm in diameter) per hectare.

Geophagous earthworms generate burrows (amongst the largest pores in many soils) with a diameter similar to their body diameter. The effect of earthworm burrowing on total porosity may depend on the bulk density of the soil horizon before earthworm activity, and whether most of the casting is deposited on the soil surface or in the same horizon from which it originated.

Although earthworm burrows may account for a small fraction of soil volume (Gantzer and Blake 1978, Lauren et al. 1988), burrow continuity is an important attribute of earthworm induced porosity (Lee 1985). Although uneven introductions of European earthworms to the U. S. over the past three centuries (Reynolds 1977) may account for population differences in similarly managed fields, soil management methods can influence earthworm densities (Gantzer and Blake 1978, Shipitalo and Protz 1987). It may, therefore, be possible and advantageous to manage the number, diameter, and length of earthworm burrows in field situations to influence air, water, and chemical movement (Smettem 1992) (see Lee this volume).

The continuity and shape of the burrow system and its access to water influence the effectiveness of burrow infiltration. Teotia et al. (1950) poured molten lead into worm holes and washed away the soil to reveal the continuity and tortuosity of the burrow system. Recently, burrow length, orientation, and branching frequency were measured during careful excavation by McKenzie and Dexter (1993).

B. Earthworm Burrows and Infiltration

The tremendous capacity of earthworm burrows for infiltration has been directly demonstrated by Bouché (1971), Ehlers (1975), and Bouma et al. (1982). Smettem and Collis-George (1985b) showed that a single, continuous 0.3 mm diameter macropore in a 100-mm diameter soil column can conduct more water than the rest of the column. Methods for evaluating porosity, including the effects of biopores on transport of water and solute, have been reviewed by Beven and Germann (1982), Nielsen et al. (1986), Wagenet (1986), Brusseau and Rao (1990), Colman et al. (1991), and Edwards et al. (1993a).

The open, vertical burrows of *L. terrestris* have been implicated in "short-circuiting" or "by-pass flow" (Bouma et al. 1981, Bouma et al. 1983, Bouma 1991). When earthworms were introduced to soil columns that had been clogged with septic tank effluent, their burrowing activity reopened the columns to flow rates greater than initial values (Jones et al. 1993). Colored dyes and other tracers have been used by investigators to confirm that flow in burrows and similar continuous macropores occurs under a wide range of conditions (Douglas et al. 1980, Tyler and Thomas 1981, Germann et al. 1984, Smettem and Collis-George 1985a, Smith et al. 1985, Everts et al. 1989, Zachmann and Linden 1989, Andreini and Steenhuis 1990).

All burrows, however, do not conduct water during all storm events (Shipitalo et al. 1990, Trojan and Linden 1992), but adding earthworms to worm-free soils usually results in increased infiltration rates (Kladivko et al. 1986). Previous soil moisture content influences flow in earthworm burrows as does rainfall intensity (Edwards et al. 1992). Frequently, only a few of the apparently open burrows conduct water ahead of the wetting front, and those few "good conductors" are active in successive storms (Edwards et al. 1992, Trojan and Linden 1992). Effective conducting burrows may be made by both anecic and endogeic species (Joschko et al. 1992).

C. Chemical Movement in Earthworm Burrows

Chemical transport in earthworm burrows has been documented for several years, but only recently have conditions under which such movement is important been given much consideration. Because water may preferentially infiltrate earthworm burrows and bypass adjacent soil, water and chemicals that

move in the burrows can be of very different quality than in the soil matrix. For example, if burrow flow occurs in nearly vertical *L. terrestris* burrows as the result of high-intensity rain storms immediately after the surface application of chemicals, entrained chemicals can be quickly carried through much of the soil without attenuation. In much of the central U. S., fertilizers and pesticides are usually surface-applied at the time of year that storms are strongest. However, after rainfall has moved the surface-applied chemicals into the topsoil, by-pass flow may be carrying relatively clean rain water past the chemical-laden soil water held in the matrix. In the latter case, flow in the earthworm burrows may be of better quality than that held or moving down in the soil matrix.

Edwards et al. (1988a, 1989) characterized earthworm burrows in long-term no-till cornfields and documented the hydrologic conditions under which nitrate infiltrated in *L. terrestris* burrows. In English pastures, moderate population densities of *L. rubellus* and *A. caliginosa* increased nitrate transport in leachate three-fold (Knight et al. 1992). Depending upon weather conditions, which influence fertilizer uptake, nitrification, and denitrification, nitrate concentrations in burrow flow can be high at any time of the year (Shipitalo et al. 1994). Bromide, a highly soluble ion, is used as a non-reactive tracer to simulate nitrate movement in transport studies. Like nitrate, bromide movement in burrows near the surface and transport below the plow layer can be greatest whenever rapid water movement is enhanced by the introduction of earthworms (Zachmann et al. 1987).

In contrast, pesticide concentrations in burrow flow are highest in the first storm following surface application. Both concentration and transport decrease in subsequent storms (Shipitalo et al. 1990) and with time between application and the first following storm (Edwards et al. 1993b). A small storm event that does not induce burrow flow reduces herbicide concentration and transport in burrow flow of subsequent storms (Shipitalo et al. 1990). Because high rainfall intensities increase the flow of water in burrows, they also increase transport of available surface-applied chemicals (Edwards et al. 1992).

Chemical composition of the burrow lining may influence solute transport through the burrows (Stehouwer et al. 1993). Distilled water poured into the top of *L. terrestris* burrows may pick up nitrate from the drilosphere, whereas herbicide concentrations may decrease during burrow infiltration (Edwards et al. 1992, Stehouwer et al. 1994). Stehouwer et al. (1993) separated burrow linings from the surrounding soil to identify the lining properties that could increase herbicide sorption and retard herbicide transport into and out of (through) the burrows.

D. Other Effects of Earthworms on Soil Structure

At a long term experiment near Guelph, Ontario, the addition of three different types of municipally-generated sludge to the soil surface for 8 years, and continuous brome grass for 18 years created a 12-cm thick A_h horizon with

significantly lower bulk density, and, increased porosity. The results of this experiment of anthropogenically-initiated faunal amelioration of soils are summarized in Figure 1: (1) soil elevation was slightly increased, (2) a new A_{11} horizon encroached on the A_p and A_e horizons, (3) the A horizon darkened because of the incorporation of organic matter, and (4) a 1-mm thick surface sludge application over a 10 x 10 cm surface was distributed as a coating on the walls of an earthworm burrow 50-cm long. Sludge application induced a large increase in populations of *L. terrestris* in the treated soils because organic matter, nutrients, and water were no longer limiting. This meant that turnover of macronutrients and physical mixing of organic matter and mineral matrix

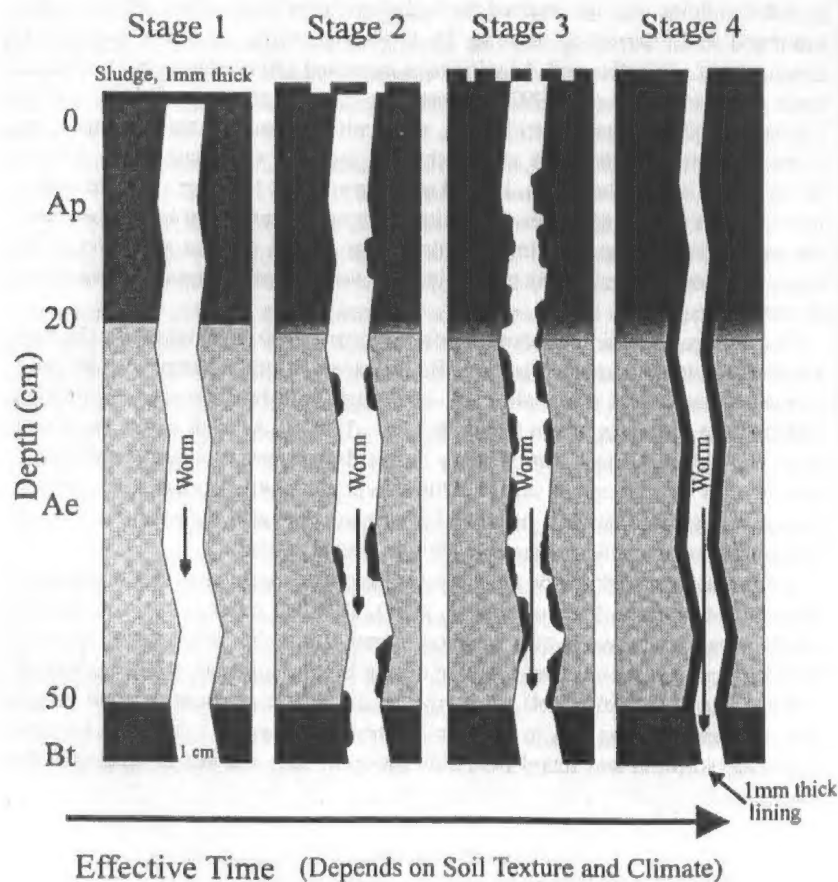


Figure 1. Proposed scheme by which earthworms transport surface applied sewage into their burrows.

were greatly accelerated by earthworms during the course of the 16 years of the experiment's duration.

E. Ingestion and Casting Activity

Earthworms are believed to be a major influence on soil aggregation because of the amounts of organic matter and soil they ingest, but quantification is difficult. The difficulty arises because measuring the size and composition of earthworm populations, their feeding and casting activities, and correlating that with type of food source and population structure under field conditions are challenging.

Field studies suggest that earthworms ingest a considerable amount of organic debris and soil. Estimates of cast production are quite variable ranging from 1.5 to 2600 Mg ha⁻¹ yr⁻¹ (Watanabe and Ruaysoongnern 1984) (note: 13 Mg represents a 1 mm thick layer of soil/ha at a bulk density of 1.3 Mg m⁻³). Guild (1955) calculates that earthworms can ingest 22 to 27 Mg ha⁻¹ yr⁻¹ of cow dung, and Satchell (1967) calculates that earthworms in a deciduous forest consume an annual leaf fall of 3 Mg ha⁻¹ in approximately 3 months. Extremely high rates of cast production are most common in tropical soils, but all estimates for temperate soils are <100 Mg ha⁻¹ yr⁻¹. It should be noted that extreme values reported for tropical areas are from old studies and may be questionable. Recently, however, Lavelle et al. (1989) reported a cast production rate of 1200 Mg ha⁻¹ yr⁻¹ in the Ivory Coast.

Nevertheless, based on available data, it is obvious that earthworms in both tropical and temperate region soils can process substantial amounts of mineral and organic material annually. Moreover, it is recognized that field estimates of casting activity are probably gross underestimates of actual amounts ingested because many species do not commonly cast onto the soil surface, and sub-surface casting is often ignored (Evans 1948, Edwards and Loft 1977 p. 145, Bal 1982 p. 12). It is logical to assume, therefore, that changes in population size, composition, or activity due to changes in cultural practices may have an effect on casting activity and soil aggregation.

Laboratory studies of feeding and casting activity overcome some of the problems inherent in field studies by controlling earthworm populations and environmental conditions. The results of laboratory studies suggest that food ingestion rate is influenced by food source (Van Rhee 1963), food supply (Raw 1962), age and chemical composition of the food (Edwards and Heath 1975), temperature (Knollenberg et al. 1985), moisture (Satchell 1967 p. 269), and earthworm species, body size, and maturity (Barley 1959a). Casting activity, in turn, is a function of feeding activity. Abbott and Parker (1981) and Martin (1982) suggest that earthworms ingest more soil in an attempt to obtain sufficient food when supply is limited, and consequently cast more frequently. Martin found, however, that some species ingest the most soil when intermediate levels of food are supplied. Under experimental conditions, Barley (1959a) and Parle (1963a) found that earthworms cast more when first placed in soil in pots,

because they are establishing new burrows and are not feeding. Abbott and Parker (1981) found that food source and food placement, as well as earthworm species, influence the amount of surface casts produced. They found that incorporating clover hay into soil results in more surface cast production by *Eisenia foetida* (Savigny) than when clover is left as a mulch on the soil surface.

Other factors affecting casting activity are soil temperature (Hartenstein et al. 1981, Joannes and Kretzschmar 1983), and soil pH and Ca levels (Springett and Syers 1984, Nielson 1951). Surface casting activity is reportedly encouraged by high soil bulk densities (Guild 1955, Thomson and Davies 1974) and influenced by soil texture (Teotia et al. 1950, Thomson and Davies 1974).

A variety of factors influence earthworm feeding and casting activity and these factors are not independent, perhaps accounting for some contradictions among studies. Ideally, it would be useful to develop a model which incorporates the key factors affecting food ingestion and casting along with measurements of field populations to predict activity in the field. However, we are a long way from achieving this goal. As a starting point, Shipitalo et al. (1988) used laboratory earthworm activity data in conjunction with field population data to calculate hypothetical food consumption and cast production rates in order to estimate the effects of food supply and food quality on earthworm populations and cast production. James (1991) estimated total cast production of mature *Diplocardia* populations in a tall grass prairie using cast production-temperature relationships obtained in the laboratory, combined with field population density estimates and soil climate data. Such approaches could be extrapolated to help us understand the changes in earthworm populations and activity that occur when land management practices are altered.

Manuring cultivated fields increases earthworm populations (Berry and Karlen 1993), and minimum tillage practices usually result in increased populations and biomass of earthworms (Edwards and Lofty 1982, De St. Remy and Daynard 1982, Berry and Karlen 1993). Crop selection and rotation have significant effects on subsequent earthworm populations with continuous soybean cropping reducing earthworm numbers the most, presumably due to the reduction in soil organic matter associated with this practice (Tomlin et al. 1993). All of these changes in earthworm populations induced by agronomic practice suggest that there could be some optimum combination of cropping and tillage practices that could be implemented to maximize earthworm numbers even to the point of manipulating species within a field that would enhance or remediate soil structure (see Edwards et al. and Lee, this volume).

III. Research Issues on Stability of Earthworm Casts

A. Methodological Issues Related to Measuring Stability

Just as the amount of material processed by earthworms is poorly quantified, so too is the aggregate stability of the food-soil mixture egested by earthworm as casts. Numerous studies assessed the stability of casts (Table 1), but we have little quantitative information on how important earthworm casting activity is in promoting soil aggregation in a natural setting.

There are a number of methods used to quantify aggregate stability and results obtained are technique dependent. Additionally, there is growing acceptance that there are different levels of organization within aggregates, and the major binding agents can differ among these levels. Edwards and Bremner (1967) first suggested that microaggregates (<250 μm) bond by different mechanisms than macroaggregates (>250 μm). Tisdall and Oades (1982) refined this concept and proposed a model that engenders several levels of aggregation to account for aggregate stability in Australian red brown earths. In their model, microaggregates are bonded by persistent, degraded, aromatic humic materials, and transient to persistent polysaccharides. Temporary binding agents, such as roots and fungal hyphae, bind microaggregates together into macroaggregates. They suggest that the model is appropriate for most soils where organic matter is the major binding agent, but the levels of aggregation may depend on soil type. Thus, different methods for measuring aggregate stability may assess aggregation at different levels, explaining why various techniques seldom yield results that are directly comparable.

Moisture status can also affect the measured stability of aggregates. Reid and Goss (1981) noted that drying of soil samples prior to assessing aggregate water stability can markedly affect measured stabilities and that the magnitude of the drying effect can be treatment dependent. Utomo and Dexter (1982) demonstrated that wetting and drying cycles and thixotropic hardening affect aggregate stability. Furthermore, Beare and Bruce (1993) have shown that the method by which samples are wetted before being subjected to wet sieving can affect the measured stabilities and the level of aggregation (micro vs. macro) being assessed. In order to avoid the effects of air drying and storage, especially when biologically mediated effects on soil structure are being investigated, they recommend that samples be analyzed immediately after sampling and that gentle pre-wetting be used. Additionally, they wisely suggest that complete specifications of the procedures used accompany aggregate stability analyses.

A further complication related to assessing the stability of earthworm casts has to do with choosing a basis by which to compare changes in stability. In field studies, casts are most often compared to soil collected nearby, which is usually coarser in texture. This can be attributed to (1) comminution of the mineral particles ingested, (2) selective avoidance by the earthworms of larger particles, and (3) ingestion of finer-texture material from elsewhere in the profile. Although some research work suggests that comminution of mineral

Table 1. Characteristics of studies in which the stability of earthworm casts was assessed.

Reference	Field/Lab Study	Location	Species	Method used to Measure Stability
Barley 1959b	Lab	Adelaide, Australia	<i>Allolobophora caliginosa</i> (Sav.)	Wet Sieving
Dawson 1947	Lab	Maryland, USA	<i>Lumbricus terrestris</i> (NS)	Falling Water Drop
Dutt 1948	Both	New York, USA	NS	Wet Sieving
Guild 1955	Lab	Edinburgh, UK	<i>Lumbricus rubellus</i> (Hoff.)	Dry and Wet Sieving
			<i>Lumbricus terrestris</i> (L.)	
			<i>Allolobophora longa</i> (NS)	
			<i>Allolobophora caliginosa</i> (Sav.)	
			<i>Dendrobaena subrubicunda</i> (Eisen)	
			<i>Hyperiophilus</i> spp.	Wet Sieving
Lal and Akinremi 1983	Field	Ibadan, Nigeria	NS	NS
Low 1972	Field	Derbyshire, UK	<i>Aporrectodea caliginosa</i> (NS)	Dispersible Clay
Marinissen and Dexter 1990	Lab	Netherlands and South Australia	<i>Aporrectodea rosea</i> (NS)	Crushing—Tensile Strength
McKenzie and Dexter 1987	Lab	Glen Osmond, South Australia	<i>Allolobophora terrestris</i> (Sav.) forma <i>longa</i> (Ude)	Permeability
Parle 1963b	Field	Rothamsted, UK	<i>Lumbricus terrestris</i> (L.)	Dispersible Clay
Shipitalo and Protz 1988	Lab	Ontario, Canada	<i>Lumbricus terrestris</i> (L.)	Wet Sieving
Swaby 1950	Field	Rothamsted, UK	<i>Allolobophora nocturna</i> (NS)	Falling Water Drop
Teotia et al. 1950	Both	Nebraska, USA	<i>Helodrilus caliginosus</i> (Sav.)	
			<i>Helodrilus parvus</i> (Eisen)	
			<i>Oecolusium lacteum</i> (Orley)	
			<i>Diplocardia riparia</i> (Smith)	
West et al. 1991	Lab	Georgia, USA	<i>Lumbricus rubellus</i> (NS)	Wet Sieving

NS — not specified in the reference.

particles occurs during passage through the gut of an earthworm (Edwards and Loft 1977), significant comminution of mineral grains during a single passage is unlikely with most materials, and they seriously question whether mineral comminution occurs. It is logical to assume that there is an upper limit to the size of mineral grains that earthworms can ingest and this size limit depends on the sizes and species of worm being investigated. Similarly, it is probable that earthworms mix material from several horizons encountered while burrowing.

Because of selective ingestion and mixing of material from elsewhere in the soil, ingested material may have different chemical and physical properties than the soil to which it is compared. Thus, it can be difficult to separate these effects from those directly attributable to the actions of the earthworms on the material ingested. This is important when the factors and mechanisms affecting aggregate stabilization in casts are being investigated. Although there is no simple way to account for this effect in the field, its potential importance must be recognized. In laboratory studies, where earthworm are confined to a uniform soil material, the mixing effect is eliminated and procedures which account for the effects of selective ingestion on aggregate stability can be used (Shipitalo and Protz 1988).

Despite the problems in quantifying the stability of casts, the existing body of research suggests that a number of factors can have an effect on stability of earthworm-formed aggregates. Both Parle (1963b) and Teotia et al. (1950) indicate that cast stability increases with age, the maximum stability being attained 15 days after excretion. Marinissen and Dexter (1990) also found that cast stability increased with age when measured up to 42 days after excretion. Conversely, Dawson (1947) reported that soil aggregates removed from the intestines of earthworms are more stable than casts and concluded that aging and post-depositional microbial activity resulted in the destruction of bonding agents and a decline in aggregate stability. Hopp and Hopkins (1946) note that aging up to four weeks caused slight decreases in the stability of casts. Shipitalo and Protz (1988) found that the effect of age was dependent on the diet provided to the worms and whether casts were dried before analysis. Unless the earthworms were provided a food source which they accepted, aging up to 32 days had no effect on cast stability.

If casts were aged moist but allowed to air-dry prior to analysis, cast age had no effect. As Shipitalo and Protz (1988, 1989) and Marinissen and Dexter (1990) demonstrated, drying can override the effect of aging on measured cast stabilities. When samples were kept moist, freshly formed casts were invariably less stable than uningested, moist, soil. It is now recognized that earthworms disrupt existing aggregates in the process of forming new ones, and restoration or improvement of aggregate strength only occurs with aging or drying (Barois et al. 1993, Lee and Foster 1991, Marinissen and Dexter 1990, McKenzie and Dexter 1987, Shipitalo and Protz 1988, 1989). Thus, for a finite period of time, casts are less stable than the soil from which they were derived. This may, in part, account for the observation that surface casting activity by earthworms contributes to soil erosion under some conditions (Madge 1969, Sharpley et al.

1979). Under some conditions wetting and drying cycles may be an important stabilization process, but air drying does not normally occur below the upper few centimeters of soil in temperate regions (Reid and Goss 1981). While wetting and drying cycles may be important for stability of surface casts, the process is probably of limited significance for subsurface casts.

Experimental evidence on the importance of food source in aggregate stabilization by earthworms is conflicting. Dawson (1947) reports aggregate stabilization in the absence of added food and that addition of lespedeza hay only slightly increased cast stability, but Swaby (1950) found that air-dried casts were more water stable than soil only when they contained "nutritive" organic matter. Teotia et al. (1950) found that worm casts were most water stable when collected from pots to which alfalfa mulch was added, less stable when from pots to which straw mulch was added, and least stable when no mulch was added. Shipitalo and Protz (1988) found that food source type provided to worms and the amount of residual organic matter remaining in casts both affect aggregate stability. In turn, the amount of organic matter incorporated into an individual cast was dependent on both food source and whether the worms were actively feeding or burrowing only. In trials where no food was provided to the worms, organic carbon originating from the worms as digestive secretions appeared to be effective in stabilizing casts, but since the amounts were small in comparison with treatments where food was provided, the effects on cast stability were minimal (Shipitalo and Protz 1988).

Earthworm species and soil texture have been shown to influence the water stability of casts. Teotia et al. (1950) found that casts produced under straw mulch by *Helodrilus caliginosus* were most stable and those of *Diplocardia riparia* least stable of four species they investigated, and that the degree of improvement in cast stability increased as soil texture became finer. Guild (1955) reported method-dependent differences in aggregate stability in soils worked by different earthworm species. Guild observed a 16 to 20%, and up to a 40%, improvement in soil aggregation due to earthworm activity for *L. rubellus* and *L. terrestris*, respectively, when assessed by the dry shaking and sieving method. When measured by wet sieving, Guild obtained a 20% and a 50% improvement for *L. rubellus* and *L. terrestris*, respectively. Shipitalo and Protz (1988) also investigated the effects of these two species on soil structure. They found that casts produced by *L. rubellus* were generally more water stable than those produced by *L. terrestris* when provided the same food source. The greater stability of casts produced by *L. rubellus* was attributed to more organic matter incorporation into their casts than those of *L. terrestris*, and not to any difference in the way these species affected soil aggregation. In a study where the interaction among species was investigated, Shaw and Pawluk (1986) found that development of soil structure was most pronounced when both anecic and endogenic species were introduced into microcosms. Aggregate stability, however, was not assessed in this study.

B. Concepts and Theories for Modeling Earthworm Cast Stability

Based on the factors which affect cast stability and ancillary data collected by investigators, numerous theories on the nature of the bonding substances and mechanisms in earthworm casts have been proposed, including:

- stabilization by internal secretions of earthworms (Dawson 1947)
- mechanical stabilization by plant fibers incorporated into casts (Dawson 1947, Lee and Foster 1991)
- mechanical stabilization by fungal hyphae (Parle 1963b, Marinissen and Dexter 1990, Lee and Foster 1991)
- stabilization by bacterial gums (Swaby 1950)
- stabilization via formation of organo-mineral bonds in the form of calcium humate (Meyer 1943 as cited by Satchell 1967, p. 294) or mucilage (Dutt 1948)
- stabilization due to wetting and drying cycles with (Shipitalo and Protz 1988, 1989) or without organic bonding (Marinissen and Dexter 1990)
- age-hardening/thixotropic effects combined with organic bonding (Shipitalo and Protz 1988, 1989).

Each of these theories probably has some validity under the conditions in which the experiments were conducted. For instance, Shipitalo and Protz (1989) suggested that drying stabilized casts due to dehydration and irreversible bonding of incorporated organic matter, whereas Marinissen and Dexter (1990) indicated that organic bonding materials did not play a major role in stabilizing dried casts. This finding must be interpreted in light of the fact that Shipitalo and Protz (1989) provided a food source to the worms, whereas no food was provided to the worms in the experiment conducted by Marinissen and Dexter (1990). The degree of aggregate stabilization detected is dependent on the properties of the soil and organic matter ingested by earthworms, the procedure by which aggregation is measured, and the level of aggregation that a particular technique assesses. None of the theories is mutually exclusive and, in all probability, more than one mechanism contributes to aggregate stabilization under field conditions. What is important is whether a particular mechanism plays a dominant role under the given set of circumstances.

Most theories assign a significant role to organic compounds as the bonding agent responsible for stabilizing the aggregates in casts. The nature of these organic compounds and the type of bonding that occurs is probably highly dependent on the chemical and physical characteristics of the food and soil ingested by the worms, and on the amount of reprocessing that occurs in the gut and subsequently in the deposited casts. Apart from these factors, it is now generally recognized that the distribution of the active fraction of the organic matter in the soil can be more important than the total amount present. For this reason a number of recent studies have utilized micromorphological techniques to investigate the distribution of organic matter in casts (Shaw and Pawluk 1986, Shipitalo and Protz 1989, Lee and Foster 1990, West et al. 1991, Altemuller and Joschko 1992, Barois et al. 1993). The general consensus derived from

these studies is that a portion of the ingested organic matter can become highly fragmented and partially humified and serve as foci for aggregate reformation. The organic substances most often implicated as bonding agents are polysaccharides and mucopolysaccharides (Shaw and Pawluk 1986, Shipitalo and Protz 1989, Lee and Foster 1991, Barois et al. 1993) but the specific composition of these substances has not been established. Based on the use of selective chemical extractants and measurement of subsequent losses in aggregate stability, Shipitalo and Protz (1989) concluded that bonding was primarily the result of Clay-Polyvalent cation-Organic Matter linkages (i.e., C-P-OM bonding of Edwards and Bremner 1967) with the materials investigated. Additionally, the type of bond formed (i.e., water bridges, cation bridges, coordination complexes) was dependent on the food source provided to the worms, and age and moisture status of the casts.

C. Earthworm Casts and Soil Structure

Only two classes of soil structure (Bullock et al. 1985, Fitzpatrick 1986), granules or crumbs (Figure 2), can be viewed as being formed dominantly by biotic processes. Individual earthworm fecal pellets could be viewed as crumbs, and casts (multiple pellets) could be viewed as granules. This scheme would fit into the hierarchy of aggregates developed by Oades and Waters (1991) and Oades (1993) (Figure 3).

The search continues for an understanding of the processes which must occur to make stable aggregates. Obviously, passage of organic material and mixing of mineral particles with a varying bacterial suite in the gut of an earthworm is part of the aggregate formation and stabilization process. Pedersen and Hendriksen (1993) concluded from data on individual bacterial concentrations that some bacteria decrease in numbers in the foregut, some bacteria increase during, and some bacteria are unaffected by passage through the gut. Earthworms exhibited selective bacterial feeding patterns that can lead to changes in bacterial survival. Stephens et al. (1993) demonstrated that the earthworm, *A. trapezoides*, in numbers comparable to field densities, transported significant amounts of the bacteria, *Pseudomonas corrugata* (strain 2140-R) from the soil surface to a depth of 9 cm in laboratory pot experiments in 9 days. This clearly demonstrates that earthworms mix organic matter and soil mineral particles together.

Heine and Larink (1993) concluded that sand and/or inorganic particles, nitrogen content and particle size of organic matter are an essential influence on the nutrition of *L. terrestris*. This would make earthworms central to soil aggregate formation. Once aggregates are formed and organic acids and enzymes interact with mineral particles, certain parts of the organic fraction are stabilized and protected by the clay and silt fractions (Figure 4, Tisdall and Oades 1982, Hassink et al. 1993). If an earthworm sac (fecal pellet) stays intact during a drying period, the bacterial decomposition products will be drawn into the silt

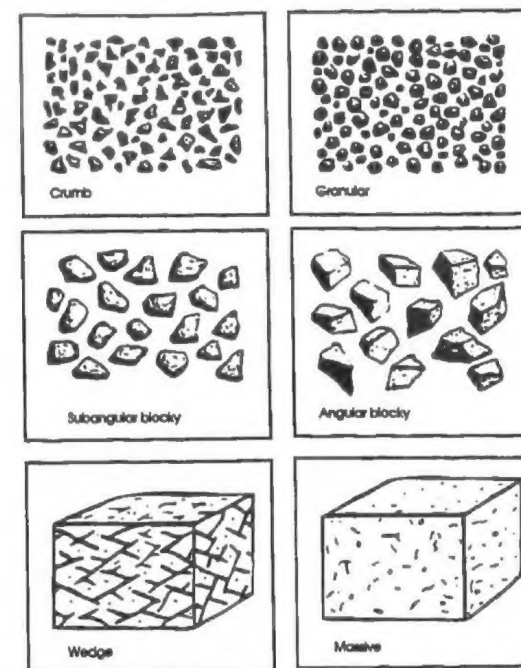


Figure 2. Diagrammatic representation of some types of soil structure (not to scale). Modified from Fitzpatrick (1986).

and clay particle interspaces as in the last stage presented by Tisdall and Oades (1982). This stable aggregate may then be reingested several times, followed by drying, resulting in the protection of older organic matter. Thus, when the surface organic matter is dated it will be modern, but internal organic matter will be older. Skjemstad et al. (1993) measured this organic matter as 200 to 320 years old. In other soils the organic matter may be older depending on the nature of soil processes forming the aggregates. Age dating will allow us to estimate the rates at which degraded A_p horizons can be rehabilitated.

Wershaw (1992) reviewed concepts of biomass degradation in soils and sediments, and proposed that depolymerization and oxidation reactions that occur during enzymatic degradation of biopolymers produce amphiphiles, molecules that have polar (hydrophilic) and nonpolar (hydrophobic) moieties. Amphiphiles resulting from partial oxidative degradation of biomass assemble spontaneously into ordered structures in which the hydrophobic moiety forms the interior of organic molecule aggregates, and the hydrophilic moiety forms the exterior surface. Amphiphiles can be viewed as micelles in solution, and at a larger, older stage of aggregation as vesicles (Figure 5). The humus-ordered aggregates in soils likely exist as bilayer membranes (Figure 5) coating mineral grains.

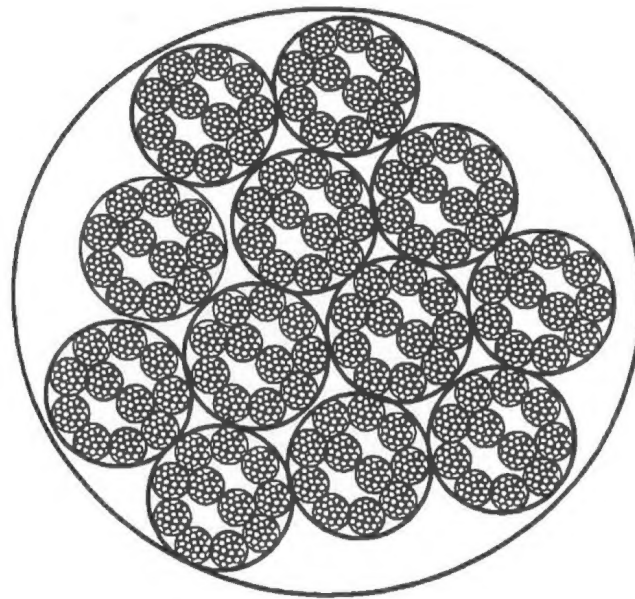


Figure 3. The concept of aggregate hierarchy. Modified from Oades (1993).

These ordered aggregates of amphiphilic molecules constitute the humus in soils. Wershaw's view of a progressive accumulation of organic molecules through the micelle, vesicle, and bilayer lipid membrane stages towards the protection of mineral particles parallels Tisdall and Oades' concepts (Figure 4). And earthworms accelerate the rate of association of organic molecules with mineral particles (Stephens et al. 1993), thus enhancing the formation of crumb and granular structure (Pedersen and Hendriksen 1993).

IV. Research Imperatives

A. Solute Transport

Effects of earthworm activity on soil porosity and water infiltration have been well documented. But we are only beginning to understand the conditions under which earthworm burrows transport solutes, particularly surface-applied chemicals, into deeper soil or groundwater. Controlled experiments under field conditions in addition to laboratory process studies are needed to address this problem.

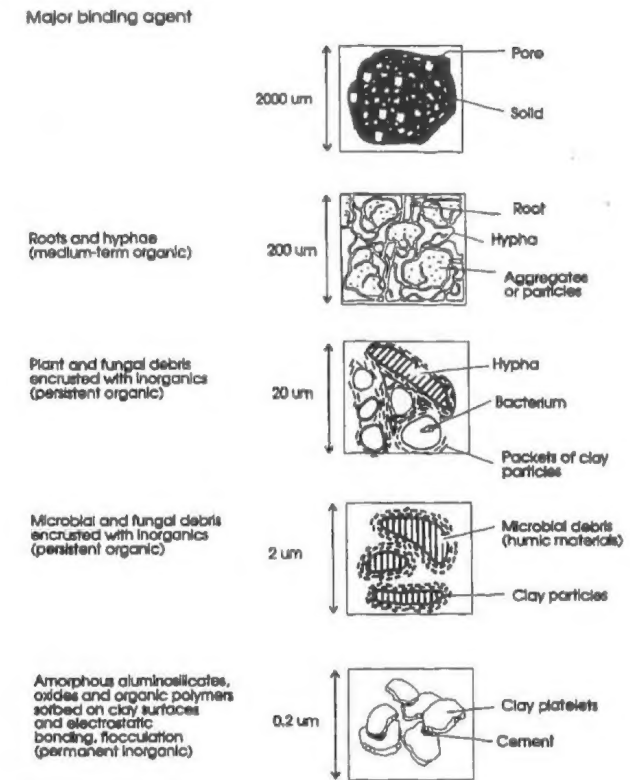


Figure 4. Model of aggregate organization with major binding agents indicated. Modified from Tisdall and Oades (1982).

B. Properties of Burrow Linings

Earthworm burrows also may function both as a source and a sink for certain compounds in water flowing through them. Research is needed to better characterize the physical, chemical, and microbiological nature of burrow linings, particularly their exchange properties and organic chemical composition.

C. Soil Processing and Soil Structure

We have no reliable data as to how much material is processed by earthworms and, given the difficulty associated with measuring this in the field, this will likely remain a problem. Rather than let this deficiency impede progress, we

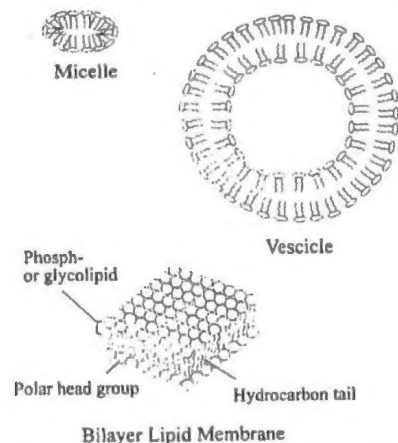


Figure 5. Diagrammatic representations of amphiphilic molecules. Modified from Wershaw (1992).

should continue to address the question of how earthworms affect soil structure, because it is obvious that earthworms process large amounts of soil and organic matter that affect soil aggregation.

D. Aggregate Stabilization

We now recognize that earthworm casting activity initially destabilizes aggregation, but net improvements in aggregate stability can occur over time. Stabilization is influenced by the amount and nature of organic matter incorporated, cast age and moisture status. What is unknown is whether these improvements in aggregate stability measured in the laboratory, or on individual casts collected in the field, translate into a net improvement in soil structure in the field (and how long any improvement persists). Under natural conditions soil aggregation is a dynamic process. Aggregate formation and destruction can occur simultaneously, and improvement in soil structure occurs when the former predominates. We know that soils with good structure and stable aggregates exist where earthworms are absent. We need to know what properties enhance aggregate stability in these soils and, conversely, in soils without these properties, how earthworm activity may impact aggregate stability. The key probably lies in the nature of organic compounds and particularly in the rate of their association with mineral particles, which is accelerated by earthworm activity.

E. Field and Laboratory Studies

In the field there are innumerable interactions among anecic and endogeic earthworms, and among earthworms and other soil-inhabiting animals, such as enchytraeids and microarthropods. Given the complexity of the soil ecosystem, perhaps the best approach to answering our questions is to study intact systems where earthworm activity has been experimentally manipulated by selectively defaunating or selecting soils devoid of earthworms, introducing earthworms or stimulating earthworm activity by altering fertility, pH, organic matter, or calcium levels (e.g., Hamilton and Dindal 1989). These studies must be long-term in order to factor out natural variations inherent in field studies and should be conducted in conjunction with controlled laboratory studies that are process-oriented.

F. Organomineral Interactions and Soil Rehabilitation

Finally, we need experiments where earthworms are fed a single plant material within a mono-mineralic soil (a pure clay mineral) to clarify the process of organic molecule-clay mineral interaction within earthworm fecal pellets, and the subsequent bacterial decomposition processes. The exact orientation of mineral grains in fine aggregates may be measured by high resolution electron microprobe X-ray backscatter images (Petruk 1989) using image analysis software such as Mocha® (Jandel Scientific 1993). In consequence, we should be able to relate the crumb/granular soil structure of different A_h horizons to soil texture and faunal activity. The rate of earthworm and associated faunal activity in never-cultivated soils could be measured using gamma isotopes (McCabe et al. 1991). Rehabilitation of A_p horizons (with massive to angular blocky structure) to " A_h horizons" with crumb and granular structure similar to no-till and/or minimum-till systems could be measured using trace elements and/or molecules following microscopic and submicroscopic techniques employed by Tomlin et al. (1993).

Acknowledgments

The authors acknowledge critical reading of the manuscript by Dr. C. Fox and the technical assistance of J. Miller, J. Fonseca, B. Vandenbygaart, G. Lambert, and library assistance of D. Drew.

References

- Abbott, I. and C.A. Parker. 1981. Interactions between earthworms and their soil environment. *Soil Biol. Biochem.* 13:191-197.

- Altemuller, H.J. 1974. Mikroskopie der boeden mit hilfe von duennschliffen (Soil microscopy with thin sections). *Handbuch der mikroskopie in der technik*. Band IV, Teil 2. Umschau Verlag, Frankfurt am Main. pp. 309-367.
- Altemuller, H.-J., and M. Joschko. 1992. Fluorescent staining of earthworm casts for thin section microscopy. *Soil Biol. Biochem.* 24:1577-1582.
- Altemuller, H.J. and B. van Vliet-Lanoe. 1990. Soil thin section fluorescence microscopy. p. 565-579. In: Douglas, L.A. (ed.) *Soil micromorphology*. Elsevier Science Publishers, Amsterdam.
- Andreini, M.S., and R.S. Steenhuis. 1990. Preferential paths of flow under conventional and conservation tillage. *Geoderma* 46:85-102.
- Baker, J.L. 1987. Hydrologic effects of conservation tillage and their importance relative to water quality. p. 113-124. In: Logan, T.J. et al. (eds.) *Effects of conservation tillage on groundwater quality: nitrates and pesticides*. Lewis Publications, Chelsea, MI.
- Bal, L. 1973. *Micromorphological analysis of soils. Lower levels in the organization of organic soil materials*. Soil Survey Papers No.6. Soil Survey Institute, Wageningen, The Netherlands.
- Bal, L. 1982. *Zoological ripening of soils*. Ctr. Agric. Publ. Doc., Report 850. Wageningen, The Netherlands.
- Barley, K.P. 1959a. The influence of earthworms on soil fertility. II. Consumption of soil and organic matter by the earthworm *Allolobophora caliginosa*. *Aust. J. Agric. Res.* 10:179-185.
- Barley, K.P. 1959b. Earthworms and soil fertility. IV. The influence of earthworms on the physical properties of a red-brown earth. *Aust. J. Agric. Res.* 10:371-376.
- Barois, I., G. Villemin, P. Lavelle, and F. Toutain. 1993. Transformation of the soil structure through *Pontoscolex corethrurus* (Oligochaeta) intestinal tract. *Geoderma* 56:57-66.
- Beare, M.H. and R.R. Bruce. 1993. A comparison of methods for measuring water-stable aggregates: Implications for determining environmental effects on soil structure. *Geoderma* 56:87-104.
- Berry, E.C. and D.L. Karlen. 1993. Comparison of alternative farming systems. II. Earthworm population density and species diversity. *Am. J. Alt. Agric.* 8:21-26.
- Beven, K. and P. Germann. 1982. Macropores and water flow in soils. *Water Resour. Res.* 19:1311-1325.
- Bouché, M.B. 1971. Relations entre les structures spatiales et fonctionnelles des écosystèmes, illustrées par le rôle pédobiologique des vers de terre. p. 189-209. In: Delamere Deboutteville, C. (ed.) *La Vie dans les Sols*. Gauthiers Villars, Paris.
- Bouché, M.B. 1977. Stratégies lombriciennes. In: Lohm, U. and T. Persson (eds.) *Soil organisms as components of ecosystems*. Ecological Bulletin (Stockholm) 25:122-132.
- Bouma, J. 1991. Influence of soil macroporosity on environmental quality. *Adv. Agron.* 46:1-37.
- Bouma, J., C.F.M. Belmans, and L.W. Dekker. 1982. Water infiltration and redistribution in a silt loam subsoil with vertical worm channels. *Soil Sci. Soc. Am. J.* 46:917-921.
- Bouma, J., C. Belmans, L.W. Dekker, and W.J.M. Jeurissen. 1983. Assessing the suitability of soils with macropores for subsurface liquid waste disposal. *J. Environ. Qual.* 12:305-311.
- Bouma, J., L.W. Dekker, and C.J. Muilwijk. 1981. A field method for measuring short-circuiting in clay soils. *J. Hydrol.* 52:347-354.

- Brusseau, N.L. and P.S.C. Rao. 1990. Modeling solute transport in structured soils: A review. *Geoderma* 46:169-192.
- Bullock, P., N. Fedoroff, A. Jongerius, G. Stoops, T. Tursina, and U. Babel. 1985. *Handbook for soil thin section description*. Waine Research Publications, Albrighton, Wolverhampton, England. 152 p.
- Coltman, K.M., L.C. Brown, N.R. Fausey, A.D. Ward, and T.J. Logan. 1991. Soil columns for solute transport studies: A review. *Am. Soc. Agric. Eng. Paper No.* 91-2150, 35 pp.
- Darwin, C. 1881. *The formation of vegetable mould through the action of worms, with observations on their habits*. Murray, London.
- Dawson, R.C. 1947. Earthworm microbiology and the formation of water-stable soil aggregates. *Soil Sci. Soc. Am. Proc.* 12:512-516.
- De St. Remy, E.A. and T.B. Daynard. 1982. Effects of tillage methods on earthworm populations in monoculture corn. *Can. J. Soil Sci.* 62:699-703.
- Douglas, J.T., M.J. Gross, and D. Hill. 1980. Measurements of pore characteristics in a clay soil under ploughing and direct drilling, including the use of a radioactive tracer (^{14}Ce) technique. *Soil Tillage Res.* 1:11-18.
- Dutt, A.K. 1948. Earthworms and soil aggregation. *J. Am. Soc. Agron.* 40:407-410.
- Edwards, A.P. and J.M. Bremner. 1967. Microaggregates in soils. *J. Soil Sci.* 18:64-73.
- Edwards, C.A. 1980. Interactions between agricultural practice and earthworms. p. 3-12. In: Dindal, D.L. (ed.) *Soil biology as related to land use practices*. EPA, Washington, D.C.
- Edwards, C.A. and G.W. Heath. 1975. Studies in leaf litter breakdown. III. The influence of leaf age. *Pedobiologia* 15:348-354.
- Edwards, C.A. and J.R. Lofty. 1977. *Biology of earthworms*. 2nd ed. Chapman and Hall, London.
- Edwards, C.A. and J.R. Lofty. 1982. The effect of direct drilling and minimal cultivation on earthworm populations. *J. Appl. Ecol.* 19:723-734.
- Edwards, W.M., L.D. Norton, and C.E. Redmond. 1988a. Characterizing macropores that affect infiltration into nontilled soils. *Soil Sci. Soc. Am. J.* 43:851-856.
- Edwards, W.M., M.J. Shipitalo, W.A. Dick, and L.B. Owens. 1992. Rainfall intensity affects transport of water and chemicals through macropores in no-till soil. *Soil Sci. Soc. Am. J.* 56:52-58.
- Edwards, W.M., M.J. Shipitalo, and L.D. Norton. 1988b. Contribution of macroporosity to infiltration into a continuous corn no-tilled watershed: Implications for contaminant movement. *J. Contam. Hydrol.* 3:193-205.
- Edwards, W.M., M.J. Shipitalo, and L.B. Owens. 1993a. Gas, water and solute transport in soils containing macropores: A review of methodology. *Geoderma* 57:31-49.
- Edwards, W.M., M.J. Shipitalo, L.B. Owens, and W.A. Dick. 1993b. Factors affecting preferential flow of water and atrazine through earthworm burrows under continuous no-till corn. *J. Environ. Qual.* 22:453-457.
- Edwards, W.M., M.J. Shipitalo, L.B. Owens, and L.D. Norton. 1989. Water and nitrate movement in earthworm burrows within long-term no-till corn fields. *J. Soil Water Conserv.* 44:240-243.
- Ehlers, W. 1975. Observations on earthworm channels and infiltration on tilled and untilled loess soil. *Soil Sci.* 119:242-249.
- Evans, A.C. 1948. Studies on the relationships between earthworms and soil fertility. II. Some effects of earthworms on soil structure. *Ann. Appl. Biol.* 35:1-13.

- Everts, C.J., R.S. Kanwar, E.C. Alexander Jr., and S.C. Alexander. 1989. Comparison of tracer mobilities under laboratory and field conditions. *J. Environ. Qual.* 18:491-498.
- Fitzpatrick, E.A. 1986. *An introduction to soil science*. 2nd ed. Longman, England.
- Gantzer, C.J. and G.R. Blake. 1978. Physical characteristics of Le Sueur clay loam following no-till and conventional tillage. *Agron. J.* 70:853-857.
- Germann, P.F., W.M. Edwards, and L.B. Owens. 1984. Profiles of bromide and increased soil moisture after infiltration into soils with macropores. *Soil Sci. Soc. Am. J.* 48:237-244.
- Guild, W.J. McL. 1955. Earthworms and soil structure. p. 83-98. In: Kevan, D.K. McE. (ed.) *Soil zoology*. Butterworths, London.
- Hamilton, W.E. and D.L. Dindal. 1989. Impact of landspread sewage sludge and earthworm introduction on established earthworms and soil structure. *Biol. Fertil. Soils* 8:160-165.
- Hartenstein, F., E. Hartenstein, and R. Hartenstein. 1981. Gut load and transit time in the earthworm *Eisenia foetida*. *Pedobiologia* 22:5-20.
- Hassink, J., L.A. Bouwman, K.B. Zwart, J. Bloem, and L. Brussaard. 1993. Relationships between soil texture, physical protection of organic matter and soil biota and C and N mineralization in grassland soils. *Geoderma* 57:105-128.
- Heine, O. and O. Larink. 1993. Food and cast analyses as a parameter of turn-over of materials by earthworms (*Lumbricus terrestris* L.). *Pedobiologia* 37:245-256.
- Hendriksen, N.B. 1990. Leaf litter selection by detritivore and geophagous earthworms. *Biol. Fertil. Soils* 10:17-21.
- Hoeksema, K.J. and A. Jongerius. 1959. On the influence of earthworms on the soil structure in mulched orchards. *Proc. Int. Symp. Soil Struct. Ghent 1958*, pp. 188-194.
- Hopp, H. and H. Hopkins. 1946. Earthworms as a factor in the formation of water-stable aggregates. *J. Soil Water Cons.* 1:11-13.
- James, S.W. 1991. Soil, nitrogen, phosphorus, and organic matter processing by earthworms in a tallgrass prairie. *Ecology* 76:2101-2109.
- Jandel Scientific. 1993. Mocha® Image Analysis Software for Windows. San Rafael, CA.
- Joannes, H. and A. Kretschmar. 1983. Model of gut transit in earthworms *Nicodrilus* spp. *Rev. Ecol. Biol. Soil* 20:349-366.
- Jones, L.A., E.M. Rutledge, H.D. Scott, D.C. Wolf, and B.J. Teppen. 1993. Effects of two earthworm species on movement of septic tank effluent through soil columns. *J. Environ. Qual.* 22:52-57.
- Joschko, M., W. Söchtig, and L. Larink. 1992. Functional relationship between earthworm burrows and soil water movement in column experiments. *Soil Biol. Biochem.* 24:1545-1547.
- Kladivko, E.J., A.D. Mackay, and J.M. Bradford. 1986. Earthworms as a factor in the reduction of soil crusting. *Soil Sci. Soc. Am. J.* 50:191-196.
- Knight, D., P.W. Elliott, J.M. Anderson, and D. Scholefield. 1992. The role of earthworms in managed, permanent pastures in Devon, England. *Soil Biol. Biochem.* 24:1511-1517.
- Knollenberg, W.G., R.W. Merritt, and D.L. Lawson. 1985. Consumption of leaf litter by *Lumbricus terrestris* (Oligochaeta) on a Michigan woodland floodplain. *Am. Midl. Nat.* 113:1-6.
- Kretschmar, A. 1987. Soil partitioning effect of an earthworm burrow system. *Biol. Fertil. Soils* 3:121-124.

- Lal, R. 1974. No-tillage effects on soil properties and maize (*Zea mays* L.) production in western Nigeria. *Plant Soil* 40:237-244.
- Lal, R. and O.O. Akinremi. 1983. Physical properties of earthworm casts and surface soil as influenced by management. *Soil Sci.* 135:114-122.
- Lauren, J.G., R.J. Wagenet, J. Bouma, and J.H.M. Woosten. 1988. Variability of saturated hydraulic conductivity in a Glossaquic Hapludalf with macropores. *Soil Sci.* 145:20-28.
- Lavelle, P., R. Schaefer, and Z. Zaidi. 1989. Soil ingestion and growth in *Millsonia anomala*, a tropical earthworm, as influenced by the quality of the organic matter ingested. *Pedobiologia* 33:379-388.
- Lee, K.E. 1985. *Earthworms, their ecology and relationships with soils and land use*. Academic Press, New York.
- Lee, K.E. and R.C. Foster. 1991. Soil fauna and soil structure. *Aust. J. Soil Res.* 29:745-775.
- Low, A.J. 1972. The effect of cultivation on the structure and other physical characteristics of grassland and arable soils (1945-1970). *J. Soil Sci.* 23:363-380.
- Mackay, A.D. and E.J. Kladivko. 1985. Earthworms and rate of breakdown of soybean and maize residues in soil. *Soil Biol. Biochem.* 17:851-857.
- Madge, D.S. 1969. Field and laboratory studies on the activities of two species of tropical earthworms. *Pedobiologia* 9:188-214.
- Marinissen, J.C.Y. and A.R. Dexter. 1990. Mechanisms of stabilization of earthworm casts and artificial casts. *Biol. Fertil. Soils* 9:163-167.
- Martin, N.A. 1982. The interaction between organic matter in soil and the burrowing activity of three species of earthworms (Oligochaeta: Lumbricidae). *Pedobiologia* 24:185-190.
- McCabe, D.C., R. Protz, and A.D. Tomlin. 1991. Faunal effects on the distribution of gamma emitting radionuclides in four forested soils. *Water, Air and Soil Pollution*, 57-58:521-532.
- McKenzie, B.M. and A.R. Dexter. 1987. Physical properties of casts of the earthworm *Aporrectodea rosea*. *Biol. Fertil. Soils* 5:152-157.
- McKenzie, B.M. and A.R. Dexter. 1993. Size and orientation of burrows made by the earthworms *Aporrectodea rosea* and *A. caliginosa*. *Geoderma* 56:233-241.
- Nielsen, D.R., M.Th. Van Genuchten, and J.W. Bigger. 1986. Water flow and solute transport processes in the unsaturated zone. *Water Resour. Res.* 22:89-109.
- Nielson, R.L. 1951. Effect of soil minerals on earthworms. *N. Z. J. Agric.* 83:433-435.
- Oades, J.M. 1993. The role of biology in the formation, stabilization and degradation of soil structure. *Geoderma* 56: 377-400.
- Oades, J.M. and A.G. Waters. 1991. Aggregate hierarchy in soils. *Aust. J. Soil Res.* 29:815-828.
- Parle, J.N. 1963a. Microorganisms in the intestines of earthworms. *J. Gen. Micro.* 31:1-11.
- Parle, J.N. 1963b. A microbiological study of earthworm casts. *J. Gen. Micro.* 31:13-22.
- Pedersen, J.C. and N.B. Hendriksen. 1993. Effect of passage through the intestinal tract of detritivore earthworms (*Lumbricus* spp.) on the number of selected Gram-negative and total bacteria. *Biol. Fertil. Soils* 16: 227-232.
- Petruck, W. 1989. *Short course on image analysis applied to mineral and earth sciences*. Mineralogical Association of Canada, Ottawa.

- Raw, F. 1962. Studies of earthworm populations in orchards. I. Leaf burial in apple orchards. *Ann. Appl. Biol.* 50:389-404.
- Reid, J.B. and M.J. Goss. 1981. Effect of living roots of different plant species on the aggregate stability of two arable soils. *J. Soil Sci.* 32:521-541.
- Reynolds, J.W. 1977. *The earthworms (Lumbricidae and Sparganophilidae) of Ontario*. Life Sciences Miscellaneous Publications, Royal Ontario Museum, Toronto.
- Satchell, J.E. 1967. Lumbricidae. p. 259-322. In: Burges, A. and F. Raw (eds.) *Soil biology*. Academic Press, London.
- Sharpley, A.N., J.K. Syers, and J.A. Springett. 1979. Effect of surface-casting earthworms on the transport of phosphorous and nitrogen in surface runoff from pasture. *Soil Biol. Biochem.* 11:459-462.
- Shaw, C. and S. Pawluk. 1986. The development of soil structure by *Octolasion tyrtaeum*, *Aporrectodea turgida* and *Lumbricus terrestris* in parent materials belonging to different textural classes. *Pedobiologia* 29:327-339.
- Shipitalo, M.J., W.M. Edwards, W.A. Dick, and L.B. Owens. 1990. Initial storm effects on macropore transport of surface-applied chemicals in no-till soil. *Soil Sci. Soc. Am. J.* 54: 1530-1536.
- Shipitalo, M.J., W.M. Edwards, and C.E. Redmond. 1994. Comparison of water movement and quality in earthworm burrows and pan lysimeters. *J. Environ. Qual.* 23:1345-1351.
- Shipitalo, M.J. and R. Protz. 1987. Comparison of morphology and porosity of a soil under conventional and zero tillage. *Can. J. Soil Sci.* 67: 445-456.
- Shipitalo, M.J. and R. Protz. 1988. Factors influencing the dispersibility of clay in worm casts. *Soil Sci. Soc. Am. J.* 52:764-769.
- Shipitalo, M.J. and R. Protz. 1989. Chemistry and micromorphology of aggregation in earthworm casts. *Geoderma* 45:357-374.
- Shipitalo, M.J., R. Protz, and A.D. Tomlin. 1988. Effect of diet on the feeding and casting activity of *Lumbricus terrestris* and *L. rubellus* in laboratory culture. *Soil Biol. Biochem.* 20:233-237.
- Skjemstad, J.O., L.J. Janik, M.J. Head, and S.G. McClure. 1993. High energy ultraviolet photo-oxidation; a novel technique for studying physically protected organic matter in clay-and silt-sized aggregates. *J. Soil Sci.* 44:485-499.
- Smettem, K.R.J. 1992. The relation of earthworms to soil hydraulic properties. *Soil Biol. Biochem.* 24:1539-1543.
- Smettem, K.R.J. and N. Collis-George. 1985a. Statistical characterization of soil biopores using a soil peel method. *Geoderma* 36:27-36.
- Smettem, K.R.J. and N. Collis-George. 1985b. The influence of cylindrical macropores on steady-state infiltration in a soil under pasture. *J. Hydrol.* 52:107-114.
- Smith, M.S., G.W. Thomas, R.E. White, and D. Ritonga. 1985. Transport of *Escherichia coli* through intact and disturbed soil columns. *J. Environ. Qual.* 14:87-91.
- Springett, J.A., R.A.J. Gray, and J.B. Reid. 1992. Effect of introducing earthworms into horticultural land previously denuded of earthworms. *Soil Biol. Biochem.* 24:1615-1622.
- Springett, J.A. and J.K. Syers. 1984. Effect of pH and calcium content of soil on earthworm cast production in the laboratory. *Soil Biol. Biochem.* 16:185-189.
- Stehouwer, R.C., W.A. Dick, and S.J. Traina. 1993. Characteristics of earthworm burrow lining affecting atrazine sorption. *J. Envir. Qual.* 22:181-185.

- Stehouwer, R.C., W.A. Dick, and S.J. Traina. 1994. Sorption and retention of herbicides in vertically oriented earthworm and artificial burrows. *J. Environ. Qual.* 23:286-292.
- Stephens, P.M., C.W. Davoren, M.H. Ryder, and B.M. Doube. 1993. Influence of the lumbricid earthworm *Aporrectodea trapezoides* on the colonization of wheat roots by *Pseudomonas corrugata* strain 2140R in soil. *Soil Biol. Biochem.* 25:1719-1724.
- Swaby, R.J. 1950. The influence of earthworms on soil aggregation. *J. Soil Sci.* 1:195-197.
- Teotia, S.P., F.L. Duley, and T.M. McCalla. 1950. Effect of stubble mulching on number and activity of earthworms. *Neb. Agr. Exp. Stn. Res. Bull.* 165:1-20.
- Thomson, A.J. and D.M. Davies. 1974. Production of surface casts by the earthworm *Eisenia rosea*. *Can. J. Zool.* 52:659.
- Tisdall, J.M. and J.M. Oades. 1982. Organic matter and water-stable aggregates in soils. *J. Soil Sci.* 33:141-163.
- Tomlin, A.D., R. Protz, R.R. Martin, D.C. McCabe, and R.J. Lagace. 1993. Relationships amongst organic matter content, heavy metal concentrations, earthworm activity, and soil microfabric on a sewage sludge disposal site. *Geoderma* 57:89-103.
- Trojan, M.D. and D.R. Linden. 1992. Microrelief and rainfall effects on water and solute movement in earthworm burrows. *Soil Sci. Soc. Am. J.* 56:727-733.
- Tyler, D.D. and G.W. Thomas. 1981. Chloride movement in undisturbed soil columns. *Soil Sci. Soc. Am. J.* 45:459-461.
- Utomo, W.H. and A.R. Dexter. 1982. Changes in soil aggregate water stability induced by wetting and drying cycles in non-saturated soil. *J. Soil Sci.* 33:623-637.
- Van Rhee, J.A. 1963. Earthworm activities and the breakdown of organic matter in agricultural soils. p. 55-59. In: Doeksen, J. and J. van der Drift (eds.) *Soil organisms*. North Holland, Amsterdam.
- Wagenet, R.J. 1986. Water and solute flux. p 1055-1088. In: Klute, A. (ed.) *Methods of soil analysis, Part I*. 2nd ed. Agron. Monogr. 9, ASA and SSSA, Madison, WI.
- Watanabe, H. and S. Ruaysoongnern. 1984. Cast production by the Megasclecid earthworm *Pheretima* sp. in northeastern Thailand. *Pedobiologia* 26:37-44.
- Wershaw, R.L. 1992. Membrane-micelle model for humus in soils and sediments and its relation to humification. U.S. Geological Survey Open-File Report 91-513. Denver, CO. 64 pp.
- West, L.T., P.F. Hendrix, and R.R. Bruce. 1991. Micromorphic observation of soil alteration by earthworms. *Agric. Ecosystems Environ.* 34:363-370.
- Zachmann, J.E. and D.R. Linden. 1989. Earthworm effects on corn residue breakdown and infiltration. *Soil Sci. Soc. Am. J.* 53:1846-1849.
- Zachmann, J.E., D.R. Linden, and C.E. Clapp. 1987. Macroporous infiltration and redistribution as affected by earthworms, tillage, and residue. *Soil Sci. Soc. Am. J.* 51:1580-1586.